EMBO reports

The impact of CO_2

The global rise in the levels of CO_2 is good for trees, bad for grasses and terrible for corals

This year's Nobel Peace Prize for former US Vice President Al Gore and the Intergovernmental Panel on Climate Change (Geneva, Switzerland) again highlighted the importance and possible threat of anthropogenic climate change by rising levels of carbon dioxide (CO_2) in the atmosphere. Worse still—and often ignored—are the effects of rising levels of CO_2 in their own right, regardless of climate change. However, research focusing on the carbon dimension is now giving a more accurate picture of how land plants and marine organisms in particular will respond to progressively higher concentrations of CO_2 in both the atmosphere and the sea.

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The impact of elevated levels of atmospheric CO_2 on land and in water will be very different but both already have scientists worried, particularly with regard to the fate of calciferous marine organisms such as corals. "On the ocean side, the effects of CO_2 rise are much more pernicious," said Ken Caldeira of the Department of Global Ecology at the Carnegie Institution of Washington, DC, USA. "For land plants, CO_2 can be thought of as an essential nutrient. There is a constant struggle [for land plants] to let in more CO_2 and let out as little water as possible. But ocean organisms are almost never limited by the availability of CO_2. They are more constrained by light or availability of nutrients."

The crucial point for marine organisms is that rising levels of CO_2 will lower the pH of their environment, which will challenge their biochemistry—particularly organisms such as corals, coccolithophores (single-celled algae), crustaceans and molluscs, all of which use calcium carbonate ($CaCO_3$) to produce external skeletons or shell coverings. Seawater is slightly alkaline, with a pH now in the range of 7.9 to 8.2 in the open ocean. This value has decreased by an average of approximately 0.1 since the beginning of the industrial era as a result of the anthropomorphic release of CO_2 into the atmosphere, which, in turn, has increased the concentration of CO_2 in the oceans. CO_2 lowers the oceanic pH by increasing the concentration of hydrogen ions (H^+) in the water. It also reacts with water to form several ionic and non-ionic species including bicarbonate ions (HCO_3^-), which are less alkaline than carbonate ions (CO_3^{2-}). The net effect is a decrease in alkalinity and a lower concentration of carbonates in the water.

The decreasing amounts of calcium carbonates threaten a wide variety of calcifying marine organisms. The timing of their potential extinction will depend largely on the type of $CaCO_3$ that they require. Corals, for example, use aragonite to build their exoskeleton, whereas many plankton organisms use calcite for protective coverings. Aragonite dissolves more easily than calcite, so there is a more immediate threat to corals and their associated reefs, including the Great Barrier Reef off the coast of Queensland, Australia, which spans an area of 344,400 square km. According to Caldeira, coral reefs could start to dissipate once the level of $CaCO_3$ falls below 3.25 times over-saturation, or as soon as atmospheric levels of CO_2 reach 550 ppm. "At current emission levels, this will happen by mid-century, perhaps even 2040," he said.

The outlook is less bleak for other calciferous organisms such as many plankton. However, even they will not be able to survive the higher levels of CO_2 that are likely if humans continue to burn significant amounts of fossil fuel; Caldeira believes that 750 ppm in the atmosphere is the upper limit in which they could survive. "In any case, as CO_2 concentrations increase […] it becomes harder for organisms with shells to build, and they need to put more energy in, leaving less for reproduction, finding food and avoiding predators," he said. Some organisms might therefore start to become extinct even before concentrations of $CaCO_3$ reach the critical point, as they will be unfit to compete against non-calciferous rivals.

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At least one organism, the pteropod, also known as the sea snail or sea butterfly—which inhabits cold waters in which CO_2 dissolves more readily—is already losing shell mass. "With respect to calcifiers, areas which already exhibit a low $CaCO_3$ saturation state will be affected first," commented Jean-Pierre Gattuso, Senior Research Scientist at the Laboratoire d'Océanographie in Villefranche-sur-mer, France. "These are high-latitude regions and deep waters."

The implications of falling oceanic pH levels are less clear for non-calciferous marine organisms because some might actually benefit from the indirect consequences of rising CO_2 concentrations. "There is some evidence that elevated CO_2 will stimulate

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primary production of some species," noted Gattuso. "There is also some recent data suggesting that nitrogen fixation will be stimulated. Winners could be identified as research progresses."

Yet, there will also be losers among non-calciferous organisms. Caldeira pointed out that rising levels of CO_2 could affect oxygen and CO_2 transport in the blood of marine organisms because the binding behaviour of haemoglobin is sensitive to blood pH. When blood enters the gills, the low CO_2 concentration there reduces the acidity and causes the pH of the blood to rise, which encourages haemoglobin to bind to oxygen and to release CO_2. As the blood circulates and oxygen is converted to CO_2, the blood pH falls and increases the ability of haemoglobin to bind to CO_2. More CO_2 in the water will decrease the pH around the gills and, therefore, allow less CO_2 to be expelled from the blood. This effect will be amplified by global warming because warm water can take up less oxygen. As Caldeira pointed out, organisms might adapt by generating more oxygen-fixating pigment, but again this could come at the expense of other fitness attributes such as reproductive ability; squid are among those most vulnerable to this threat (Caldeira *et al*, 2005).

The impact on higher animals—including fish and marine mammals—will be far less because their body chemistry is insulated against the external ocean to a much greater extent than most non-vertebrates. However, higher organisms might still be affected indirectly because they rely on other organisms lower down the food chain. Ove Hoegh-Guldberg, Professor and Director of the Centre for Marine Studies at the University of Queensland, Australia, noted that, "[g]iven that these lower organisms provide the photosynthetic energy that ultimately passes through important organisms such as krill, fish and eventually large organisms such as sea mammals, there is growing concern about the impact on food chains."

There is less concern about the impact of rising levels of CO_2 in the atmosphere on land food chains, although scientists also expect to see profound changes. While primitive animals are bearing the brunt of the CO_2 onslaught in the oceans, it will be plants that are mostly affected on land. The difference for plants is that CO_2 is, in effect, a fertilizer, and could boost growth rates and reproduction across a wide range of plant species. But the spoils of raised atmospheric CO_2 concentration will not be divided evenly across the plant kingdom.

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Plants require CO_2 for photosynthesis, but they must balance CO_2 uptake through their stomata with water loss to the atmosphere. Plants that have evolved in different climates have therefore evolved different strategies to optimize the time they need to take up atmospheric CO_2. The idea that weeds will prosper under raised levels of CO_2 at the expense of crops and cultivated plants has gained wide currency, but it is an oversimplification; the response of a plant to rising levels of CO_2 will actually depend on its mechanism of photosynthesis, rather than whether humans regard it as a pest.

Plants can be divided into two categories—C_3 and C_4—based on their method of fixating CO_2 from the atmosphere, with a further subcategory of C_4 called CAM (crassulacean acid metabolism). The bulk of plants, accounting for 99% of the sum total biomass, use the C_3 mechanism to fix carbon from atmospheric CO_2, whereas most of the world's 'worst' weeds—those that are most troublesome for cultivated crops—are C_4 plants (Holm *et al*, 1978). However, it is not entirely clear whether C_3 or C_4 plants will benefit most from raised levels of CO_2, although the consensus is that C_3 plants are likely to be the overall winners (Li *et al*, 2007).

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The process is called the C_3 pathway because the first product of CO_2 reduction in photosynthesis is a 3-carbon compound. The enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) regulates the uptake of CO_2 and the rate of photosynthesis in a single-staged process, similar

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to opening and closing the vent of a fire. This relatively straightforward mechanism imposes a lower metabolic cost than the C_4 mechanisms and is well adapted for plants in cool, moist conditions under normal light levels. All plants were thought to use this mechanism until the 1960s when Marshall Hatch and Roger Slack discovered the C_4 mechanism (Hatch & Slack, 1966).

C_4 plants evolved in arid conditions where light is plentiful but moisture is scarce, thus requiring a more efficient method for reducing water loss. C_4 plants still use rubisco to control photosynthesis, but the primary step of carbon fixation uses the enzyme phosphoenolpyruvate carboxylase (PEPC) to produce a 4-carbon compound. PEPC fixates CO_2 much faster than rubisco during times of strong sunlight, and therefore reduces water loss as the plant can close its stomata much earlier. However, the additional step consumes energy and C_4 plants are less well adapted to cooler, wetter conditions. The C_4 category includes approximately 3,000 known species in 19 plant families, including saltbush, corn, many plants that flower in summer, and grasses in arid and tropical regions. Finally, CAM plants—such as many succulents including cacti, agaves and some orchids—evolved an even more specialized adaptation for extremely arid conditions. CAM plants open their stomata only at night in order to reduce water loss; however, as photosynthesis requires the energetic input of sunlight, CAM plants convert CO_2 into an acid during the night for storage. The reaction is then reversed the next day to bring back the CO_2 for photosynthesis.

Crucially, elevated CO_2 should stimulate growth in C_3 plants and reduce the time that they need to keep their stomata open for photosynthesis. This would, in turn, reduce water loss and allow C_3 plants to flourish in more arid areas. C_3 plants, including trees, might therefore be able to spread into semi-arid areas, such as tropical savannahs, where grasses now predominate.

This analysis assumes that increased levels of CO_2 will have no further biochemical effects that might influence the fates of plant species. In the real world, however, increased levels of CO_2 might also affect the competitiveness of some plants against rival plants, disease resistance and their ability to fend off animal predators. Although this research only began in the 1990s, a few examples have already been found of how plants, including crops, could suffer under increased atmospheric CO_2.

The soybean, for example, becomes more attractive to Japanese beetles when exposed to elevated levels of CO_2, according to research by Jorge Zavala and colleagues at the Institute for Genomic Biology at the University of Illinois (Urbana, IL, USA). They compared soybeans growing at an ambient CO_2 level of 370 ppm, and plants fumigated to 550 ppm CO_2—the level of CO_2 in the atmosphere predicted by the year 2050. The elevated CO_2 affected the levels of soybean defence compounds that usually inhibit digestive enzymes in the beetles' gut and make the plant unappetizing (Zavala *et al*, 2007). "Jasmonic acid and ethylene are hormones related to the expression of the defence compound CystPI […] I found that elevated CO_2 down-regulated the expression of *lox* and *acc* synthase, which are the genes that code for the crucial enzymes in the pathway of each of those hormones. In addition, I found that elevated CO_2 down-regulated the expression of the two inducible CystPI soybean genes together with the activity of the protein," Zavala said. He also suggested that this effect was not confined to soybeans and that at least 50% of the predicted increased crop yield resulting from higher CO_2 concentrations could be consumed by predatory insects exploiting the lowered resistance of the plants.

However, in cooler climates, where there are fewer insect predators, agriculture might benefit from another possible effect of elevated CO_2—increased resistance to the cold. As noted previously, higher levels of CO_2 will allow plants to lose less water during CO_2 acquisition, which will, in turn, reduce the loss of heat through evaporation.

But increased yields might not be as great as experiments suggest because other nutrients, particularly nitrogen, might become a constraint. Recent experiments conducted by Peter Reich and colleagues at the University of Minnesota in St Paul, MN, USA, on grasses suggests that nitrogen depletion will become a significant dampener on plant growth as CO_2 levels rise (Reich *et al*, 2006).

As in the oceans, the impact of elevated atmospheric CO_2 on higher land animals is much less clear, with few direct consequences expected in the foreseeable future. There is evidence, however, that humans could also suffer, quite apart from the economic and environmental impact of climate change. A recent study by Paul Beggs and colleagues at Macquarie University, New South Wales, Australia, has found that rising CO_2 stimulates the production of pollen—particularly allergenic pollen—to an even greater extent than it boosts growth (Becks & Bambrick, 2005). This could increase the prevalence of asthma and incidence of allergic conditions such as hay fever.

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There are many other subtle changes that would affect animals that feed on plants. Some research suggests that the nutritional balance will be changed, with higher levels of starch and possibly reduced levels of protein. However, much more research is needed to understand the complex reactions of the biosphere to rising CO_2 levels—research that is now still more or less in its infancy. The one thing that is certain is that the world will change dramatically, with greatest concern about the fate of the oceans and marine life.

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